

Notes on Cofounded Nests in Three Species of Social Bees in the Genus *Exoneura* (Hymenoptera; Anthophoridae)

BY MICHAEL P. SCHWARZ*

Abstract

Trap nesting indicates that most newly founded nests of *Exoneura bicincta*, *E. richardsoni* and *E. bicolor* are inhabited by more than one adult female. One cofounded nest of an unidentified *Exoneura* species was also found. Cofounding is therefore common in at least several allodapine bees and may not have been recognized in others because of the lack of trap-nesting procedures. This may require the reinterpretation of some published data. Cofounded nests of *E. richardsoni* appear to be initiated at varying times throughout the year and may contain both eggs and pupae, suggesting that some eusocial colonies may be derived from cofoundress associations.

Introduction

In many species of social bees for which adequate data is available, colonies are derived from singly founded nests (i.e. haplometrosis), or in some socially advanced species, by a single queen accompanied by a swarm of workers (Michener 1974). Haplometrosis ensures that future colony members are related and therefore facilitates the evolution kin-selected altruism. Cofounding is comparatively rare, but has been reported for a few halictine bees (Abrams and Eickwort 1981; Michener and Lange 1958a,b; Packer and Knerer 1986; Kukuk pers. comm.). In recent years, cofounding has also been reported for several xylocopine bees from Taiwan and Japan, although the frequency of cofounded nests among newly built nests as a whole has been low (*Ceratina japonica*, 1.3%, $n = 230$, Michener 1985; *Braunsapis sauteriella*, 9.1%, $n = 66$, Maeta *et al.* 1985). However, recent work on an Australian allodapine bee, *Exoneura bicolor*, indicated that the

majority of newly founded nests in a natural population contained more than one adult female, with a maximum of eight cofoundresses per nest (Schwarz 1986, 1987). Furthermore, cofoundresses were found to be closely related to each other, indicating a high degree of kin association during founding. This finding has consequences for evolution of sociality because it demonstrates that colonies of related females can arise by joining and accepting behaviour, rather than through development of singly-founded nests. In this paper I present some preliminary findings demonstrating that cofounding is common in two other species of *Exoneura*, and occurs in a fourth.

Methods

Nests were collected from the study site used by Schwarz (1986) in the Sherbrooke Forest Park near Belgrave, Victoria. Four allodapine bees occur in this area, *E. bicolor*, *E. richardsoni*, *E. bicincta* and an unidentified species (referred to here as *Exoneura* sp. 1). Voucher specimens of all four species are deposited in the Australian National Insect Collection, Canberra. All species utilize dead fronds of the tree fern *Dicksonia antarctica* as nesting sites. In August and September 1985 approximately 500 trap nests were set out among nesting aggregations around tree ferns. Trap nests were simply dead, dry fern fronds which did not contain *Exoneura* nests and were marked with coloured plastic tape. Brood of all *Exoneura* spp. in the study area do not reach adult eclosion until mid-January. Therefore, all adults found in trap nests before mid-January were assumed to be foundresses rather than mature brood raised *in situ*.

Trap nests were collected between 18 December 1985 and 9 January 1986, either before sunrise or during periods of rain, and consequently all nestmates were assumed

*Department of Zoology, Monash University, Clayton, Victoria 3168, Current address: Department of Zoology, La Trobe University, Bundoora, Victoria 3083.

present. To determine larval placement within nests, unopened nests were cooled to 4°C (adult movement ceases at this temperature) and a small volume of diethyl ether was pipetted into the nest to anaesthetize adults. These nests were then split open, taking care not to disturb the positions of nest occupants.

Females were fixed in Kahle's Solution for at least 8 days before dissection in 70% ethanol. Ovarian development of females was measured and the presence of any endoparasites noted. Some females exhibited a pathological condition in which ovaries were replaced to various extents by a white granular material (Schwarz, 1986). Wing wear, used as an indication of flight activity was measured by counting the number of nicks in the margins of both forewings.

Results

Dissection data and nest contents for all newly founded nests of *E. bicincta*, *E. richardsoni* and *Exoneura* sp 1. are given in Table 1.

Nest architecture and placement of immatures within nests is similar to that described for *E. bicolor* (Schwarz 1986). Eggs are laid in a common clump at the bottom of the nest lumen and larvae usually occur in a contiguous group in the rear portion of the nest. Occasionally, when brood sizes are large, there may be spaces between eggs and larvae or between groups of larvae. Irregularly shaped pollen balls were distributed among groups of smaller larvae, and two smaller larvae were often found feeding from a single pollen mass. Older larvae usually fed from a pollen mass placed on their venters, though in some nests two fourth instar larvae were observed feeding from a common pollen mass. In a few nests of *E. richardsoni* pollen balls were found in the bottom of the nest lumen away from brood. Pollen balls were also found in two nests where larval eclosion had not commenced and may represent a form of food storage.

Discussion

Most newly founded nests of *E. richard-*

soni and *E. bicincta* collected were occupied by more than one foundress. Available sample sizes are too small to determine the distribution of colony sizes or place an upper limit on the number of foundresses that may occupy a single nest. Furthermore, it is likely that some nests of *E. richardsoni* had already suffered adult mortality. For example, nests 14, 17, 19, 20, 22 and 35 all contained advanced brood, yet foundresses had little or no wing wear. Hence it appears that in some nests initial colony sizes were larger than at the time of nest collection.

The small number of nests available and the restricted sampling period makes it difficult to characterize sociality in these species. However, some comparisons with *E. bicolor* can be made. Unlike *E. bicolor*, nests of *E. richardsoni* appear to have been initiated at widely different times during spring and early summer. For example, nests 15, 24 and 29 contained eggs only, although some other nests (17, 20, 22, 26 and 35) contained pupae. This apparent disparity in timing of nest initiation also occurs in *E. bicincta* (cf. nests 3, 5, 9, 10 and 11). *E. richardsoni* further differs from *E. bicolor* in that in some nests there is a wide range in developmental stages of brood. Both eggs and pupae or prepupae were found in nests 17, 19, 21, 22 and 26). Such an overlap of generations in other species may give rise to (temporarily) eusocial colonies (Michener 1965, 1974, 1985), allowing the possibility that eusociality may arise in cofounded nests in *E. richardsoni*.

Measurement of wing wear suggests that not all females engage in foraging activity to the same extent. For example, wing wear varies widely among nestmates in nests 3 and 8 (*E. bicincta*) and 13, 21 and 23 (*E. richardsoni*). There does not appear to be any consistent relationship between wing wear and ovarian size. For example, *E. richardsoni* females with enlarged ovaries were found with very worn wings (nests 13, 25 and 29) or little worn wings (nests 14 and 18). Similarly, females with small to minute ovaries ranged from high wing wear (nests 23 and 28) to little or no wing wear (nests

Table 1.

NEST No!	ADULT DISSECTION DATA	Eggs	NUMBER OF IMMATURES				DATE	
			Larvae			Prepupae		Pupae
			Small	Med.	Large			
<i>Exoneura</i> sp. 1								
1	Ar+1, Ar+4	6	-	-	-	-	30.XII	
<i>E. bicincta</i>								
2	Br+4, Dr+0	3	2	3	3	-	18.XII	
3	A+9, Br+1, D+5, D+0	6	3	-	-	-	18.XII	
4 1	P?3	-	-	-	-	-	21.XII	
5	Dr+6	4	-	-	-	-	21.XII	
6	P-7, Dr+2	2	5	-	-	-	21.XII	
7	Dr+12	-	-	-	-	-	30.XII	
8	DPr+14, Dr+3, Ir?4, Dr+4	-	-	4	3	-	30.XII	
9 1	Cr+9, P?3, E+16	-	-	-	9	6	30.XII	
10	A+8, Br+7	6	-	-	-	-	9.1	
11	E+11	-	-	1	-	2	9.1	
<i>E. richardsoni</i>								
12	Cr+0, Dr+0	8	5	1	-	-	18.XII	
13	AP+16, B-4, BPr+0	5	1	2	4	-	18.XII	
14	A+1, D+1	5	1	5	1	-	18.XII	
15	Cr+11	3	-	-	-	-	18.XII	
16	Cr+0	-	-	-	-	-	18.XII	
17	Dr+0, Dr+2	1	2	2	2	2	21.XII	
18	A+3, Dr+2, Dr+2	8	2	4	1	-	21.XII	
19	Cr+0, Cr+0	6	1	-	2	4	21.XII	
20 1	CP+1, D+3	-	-	-	-	-	6	
21	Cr+15, D+1	1	-	-	-	3	21.XII	
22	Cr+0, Dr+0, Ir-0	4	1	1	3	4	30.XII	
23	Cr+2, Ir-10	4	1	4	-	-	30.XII	
24	B+4, Cr+0	1	-	-	-	-	30.XII	
25 1	A+20	9	-	-	-	-	30.XII	
26 1	Cr+2, Dr-3, Ir+3	3	5	1	5	1	30.XII	
27	B+2	-	-	-	-	-	30.XII	
28 1	E+13	-	-	1	2	-	30.XII	
29	Ar?20, Dr??	7	-	-	-	-	31.XII	
30	Cr-13	-	-	-	-	-	3.1	
31	Dr+2	-	-	-	-	-	3.1	
32	Cr+8	-	-	-	2	-	3.1	
33	Br+9	-	-	-	-	-	9.1	
34	Dr+1, Dr+4	-	-	-	4	4	9.1	
35	P+0	-	-	-	-	-	2	

Contents of newly founded nests of three species of *Exoneura*. Table gives the number of adult females and brood of varying developmental stages, as well as the ovarian condition, insemination status and wing wear of each foundress.

1: An '1' following the Nest number indicates that an adult female of the cuckoo bee *Inquilina* (Michener 1983) was present in the nest.

?: Ovarian condition and wing wear of adult females. For each foundress ovarian condition is indicated by capital letters thus: 'A' - ovaries enlarged with at least one oocyte near egg-size, 'B' - ovaries enlarged, but non near egg size, 'C' - ovaries medium sized (largest oocyte less than half length of mature oocyte), 'D' ovaries small with terminal oocytes restricted to anterior half of ovary and 'E' - ovaries pedunculate and oocytes minute. 'P' indicates a pathological state, either presence of endoparasites or ovary granulation. 'r' indicates resorption of terminal oocytes. Presence/absence of sperm in the spermatheca is indicated by +/- . Number of wing nicks for each female is given in arabic numerals. If a particular variable, eg. wing wear, was not measurable, a '?' is given in its place.

22, 26, 31 and 34). Disparity in ovarian size of females within a single nest (eg. nests 3, 14, 18 and 29) suggests that reproductive differentiation may occur among cofoundresses. However, this difference could also be due to the disjunct egg-laying periods of nestmates. If reproductive differentiation does occur, comparison of sociality in these species with *E. bicolor* (where reproductive differentiation among cofoundresses is absent) may allow factors facilitating evolution of castes in allodapine bees to be identified.

Findings presented here indicate that cofounding is common in at least three species of *Exoneura*, and occurs in a fourth. It is possible that cofounding also occurs in other species, but has only been recognized here because of trap-nesting. This has consequences for the development of sociality in subsequent nest re-use, since cofounding will decrease mean intra-colony relatedness in subsequent colony stages. Michener (1971, p. 227) has noted that his discussion of group behaviour of African allodapine bees rests on the assumption that females do not readily join nests of conspecifics.

The possible existence of reproductive differentiation in *E. richardsoni* is interesting and may allow testing of the hypothesis (Schwarz 1987) that lack of reproductive castes in cofounded nests of *E. bicolor* is due to rapid egg production and stockpiling. Studies on sociality in *E. richardsoni* and *E. bicincta* may yield some valuable information on what factors facilitate the evolution of social behaviour.

REFERENCES

- Abrams J, Eickwort GC (1981) Nest switching and guarding by the communal sweat bee *Agapostemon vivescens*. *Insectes Soc.* 28:105-116
- Knerer G (1983) The biology and social behaviour of *Eurylaeus linearis* (Schenck). *Zool. Anz.* 211:177-186
- Maeta Y, Sakagami SF, Michener CD (1985) Laboratory studies on the life cycle and nesting biology of *Brausapis sauteriella*, a social xylocopine bee. *J. Sociobiol.* 10:17-41
- Michener CD (1965) The life cycle and social organization of bees of the genus *Exoneura* and their parasite *Inquilina*. *Univ. Kansas Sci. Bull.* 46:317-358
- Michener CD (1971) Biologies of African allodapine bees. *Bull. Amer. Mus. Natur. Hist.* 145:221-301
- Michener CD (1974) *The social behaviour of the bees*. The Belknap Press of Harvard Univ. Press, Cambridge, Mass.
- Michener CD (1983) The parasitic Australian allodapine genus *Inquilina*. *J. Kansas Entom. Soc.* 56:555-559
- Michener CD (1985) From solitary to eusocial: need there be a series of intervening species? in B Holldobler & M Lindauer (eds.) *Experimental Behavioural Ecology and Sociobiology*. Gustav Fischer Verlag, Stuttgart
- Michener CD, Lange RB (1958a) Observations on the behaviour of Brazilian halictid bees, III. *Univ. Kansas Sci. Bull.* 39:473-505
- Michener CD, Lange RB (1958b) Observations on the behaviour of Brazilian halictid bees, I. *Pseud-agapostemon*. *Ann. Entom. Soc. Amer.* 51:155-164
- Packer L, Knerer G (1986) The biology of a subtropical population of *Halictus ligatus*. I. Phenology and social organization. *Behav. Ecol. Sociobiol.* 18:363-375
- Schwarz MP (1986) Persistent multi female nests in an Australian allodapine bee *Exoneura bicolor*. *Insectes Soc.* 33:258-277
- Schwarz MP (1987) Intra-colony relatedness and sociality in the Australian allodapine bee *Exoneura bicolor*. *Behav. Ecol. Sociobiol.* (in press).

Proposed Management Plan for the Dandenong Ranges National Park

The Department of Conservation Forests and Lands is inviting comment on this management plan, which specifies conservation and management practices, levels of use and further developments to be undertaken in the park.

Copies of the plan are available from the Information Centre, DCFL, 240 Victoria Pde., East Melbourne 3001 (\$4.00 or \$5.50 posted).

Written submissions are due by March 31, 1988.